**4.1 Final publishable summary report**

Executive summary

Following project departure away from Bayesian population models, we based our research design around integral projection models ([IPMs, see Coulson 2012](#_ENREF_3)), which are similar to Bayesian approaches in flavour but allow insight into both demography and evolution by linking species life history to a trait, such as body size. IPMs also allow for an easy and insightful decision framework, simply by allowing the simulation of multiple management strategies.

The first research achievement was an invited paper to the *Raffles Bulletin of Zoology*, where the Fellow (Traill) explored global ungulate species richness, and drivers of localised extirpation. We then developed a generalised IPM for ungulates based on data across numerous ungulate species sourced from both the literature and data available from long-term studies on ungulate populations. This work, in review at *American Naturalist* allows insight into both the ecological and evolutionary outcomes of management intervention on an ungulate species of any size, up to ~500 kg. This allows biologists working on say African ungulates, where vital rate data are unavailable, opportunity to test the effects of hunting, or translocation on species population demography (such as population growth rate, female reproductive output), as well as trait change, such as body size.

Further to that, we collaborated with researchers at Sherbrooke University in Canada to develop a two-sex IPM for bighorn sheep (*Ovis canadensis*). We used a 40 year individual-based dataset to parameterise the model, and this in turn allowed insight into the effects of trophy hunting on bighorn sheep, including shifts in body size following selective harvest. This work has been written-up as a research paper and following co-author approval will be submitted to *PLoS Biology*. Another manuscript is also being prepared based on differences in age-structured or non-structured models, again with outcomes for decision-making.

Research findings have been presented at three international conferences, and the Fellow has been awarded a further Fellowship to travel to the University of Queensland, Australia.

Project description

As outlined in the mid-term report, the research objectives changed following the start of the project. This was in part due to the Fellow deferring the project for one year, and his exposure to alternate quantitative methods.

Research objectives, as outlined in the research proposal, were to develop a Bayesian decision analysis framework for endangered species (with emphasis on African rhinos), and structured around Bayesian population models. Once developed, these models were to be used within a decision-framework, with ‘decisions’ meaning management strategies such as translocation, or the failure of conservation management through illegal harvest. Initial model parameterisation was to be done through experimental manipulation of soil-mite (*Sancassania berlesei*) populations in a controlled laboratory setting. By ‘parameterisation’ - we intended to test model accuracy based on how well these (the models) predicted soil-mite population outcomes, when manipulated. After the project started in March 2011, the objectives changed to:

1) The development of a generalised IPM, based on all available life history data across ungulate species, allowing a decision framework for ungulates where data aren’t available, including harvest or translocation as described above.

2) Development of a two-sex IPM (in collaboration with Susanne Schindler, a mathematician based in the Coulson Group), and subsequent parameterisation based on long-term individual based data for an ungulate species subject to recreational harvest.

IPMs make a unique departure, however from Bayesian population models in that IPMs link demography to a heritable trait, such as body size, or even, in the case of ungulates, horn size. By doing so, the ramifications of management strategies such as selective harvest, or translocation can be tracked at both the demographic level (as per the Bayesian models that we originally proposed), but also at an evolutionary level, with outcomes for heritable traits tracked through time ([for example Coulson *et al.* 2011](#_ENREF_4)). This means that models developed for say rhino, can easily be adapted to say elephant (*Loxodonta africana*), or roan antelope (*Hippotragus equinus*) or indeed any endangered ungulate that faces selective pressure through hunting, or illegal harvest. These IPMs can then test both demographic outcomes of endangered species under pressure (as we originally intended to do), but outcomes for a trait such body size, or horn (or trophy) size.

The relevance of this is that previous research has shown that unrestricted selective harvest can lead to individuals - and horns - becoming smaller over time ([Coltman *et al.* 2003](#_ENREF_2)). A shift in the distribution of body mass within a population can have subsequent demographic effects ([Ozgul *et al.* 2009](#_ENREF_5)). Moreover a decline in ungulate trophy size may have ramifications for conservation, given that proceeds from recreational harvest are directed toward conservation effort ([Palazy *et al.* 2012](#_ENREF_6)).

Illegal harvest is also selective, in that rhinos with large horns are likely to be killed, or further, the social structure of rhino populations will be disturbed following offtake of mature individuals, with smaller males gaining reproductive access to females. These can all be factored into models.

Following the decision to base decision-making models on IPMs, the Fellow developed a generalised ungulate IPM, with this model acting as a decision-framework for harvest or changes to social structure. We found that the generalised model based on data through literature review did not provide for realistic model output, but that averaged data from long term studies provided for a robust generalised IPM (more detail provided in results section). This allowed simple and fast testing of different outcomes for management decisions for numerous ungulates.

We also tried to develop population models for African rhino populations, given the current poaching crisis in southern Africa. The Fellow travelled to South Africa and Zimbabwe in 2011, and established a collaborative link with the Lowveld Rhino Trust in Zimbabwe, but in the end their data were not comprehensive. This is because the funds required for long term, individual-based studies ([see Clutton-Brock & Sheldon 2010](#_ENREF_1)) are relatively scarce across southern Africa.

We therefore shifted focus toward ungulates where these data were available, especially where data were also available for hunted populations, and where body mass were recorded. For this we set up collaboration with the Alpine Ungulate Research Project at the Université de Sherbrooke, and they made available a 40-year dataset for bighorn sheep. As a consequence, we developed a two-sex IPM for bighorn sheep, and used the IPM as a decision framework to test various harvest scenarios, with outcomes for body and horn size. This work builds on previous key studies done on bighorn sheep, but using different techniques and where harvest was shown to force a decline in both sheep body and trophy size through time. We found that body size is not strongly heritable in male bighorn sheep and that shifts in body size through hunting have most likely been indirect, such as through shifts in population age- and sex-structure. While bighorn sheep are not endangered, the theory that we develop for the big-horn sheep two-sex IPM can easily be adapted to endangered ungulates, with important outcomes for endangered species management and conservation.

Principal findings

The major results of the research done here are outlined below, and formatted as per each paper published, or in submission.

1. Although not part of the original research proposal, the Fellow was invited to submit a research paper as part of a *special edition* for the *Raffles Bulletin of Zoology*. This work, published in 2012, explored the extent of ungulate diversity globally, and additionally explored the drivers of vulnerability among bovid species. We found that there is a clear skew of ungulates toward tropical Africa, and that the principal correlate of localised extinction in bovids was body size, followed by the extent of dietary specialisation, by a species.
2. The generalised ungulate IPM has been submitted to *American Naturalist*, and is still in review. As mentioned above, this research comprised of two parts, *viz*. localised data based on literature review, and averaged data, based on long term studies of 14 different ungulate species.
   1. The literature review was extensive and in the end we compiled a dataset based on over 500 sources from both the primary and grey literature. We thus sourced all data pertaining to ungulate survival and recruitment as a function of body mass, change in mass through time and inheritance (of juvenile mass from parents). These data allowed parameterisation of a broad IPM, and thus model development for an ungulate of any given body size. In the end, model output was unrealistic and we therefore concluded that density-dependent and –independent factors unique to each population accounted for the variation in data, and thus lack of a robust general model.
   2. We then decided on an alternate approach, and sourced data on separate ungulate species that have been the basis of long-term individual based studies. These high quality data were available through the CNRS Lyon. To attempt to account for density-dependent effects, we averaged survival and fecundity as a function of mean mass across populations, and did the same for change in mass through time, and inheritance. These data allowed another generalised model, as above, but in this instance we found that model output was realistic, for small to large sized ungulates. The next step is to validate this model, based on data available for temperate ungulate species. The Fellow has prepared research proposals to follow this up, along with a proposal to then incorporate climatic shifts within the model, but these proposals have, to date, failed to get funding.
3. Two-sex IPM exploring the effects of harvest, pending submission to *PLoS Biology*. We collaborated with a mathematician based at Imperial College (Dr Susanne Schindler), along with scientists at the University of Sherbrooke, Canada to develop a two-sex IPM for bighorn sheep. We used available data on trophy hunting to simulate harvest, and explored the outcomes of this on body mass. We found that body mass is passed-on principally by females, not males and this suggests that hunting affects change in mean mass through shifts in population age and sex structure and not directly through genetic effects.
4. Following on from the above work, the Fellow and Schindler presently prepare a follow-up manuscript based on the above data for bighorn sheep, but where the model is based on a) age structure and b) no age structure. Differences in model output will be compared, and will be the basis of a manuscript where the target journal is *Biology Letters*.
5. Finally, the Fellow supervised two MSc students through Imperial College. One of these students, Marcella Chelli currently prepares a paper for *Animal Conservation*, based on her research. She used the Safari Club International Database to source data on all trophies of all ungulates hunted globally across the past 30 years. After standardising the data, she used generalised linear mixed models to determine temporal change in trophy size as a result of hunting. She found no substantial change in horn size across hunted ungulates over the last 30 years, but did not a dramatic shift in African elephant tusk size (although elephants are not ‘true ungulates’, we included them here), and most likely as a result to disruption to the population (in particular age) structure of a long-lived animal, like elephant.

Potential impact

The research outlined here, while principally published through the peer-reviewed literature, is relevant at a number of levels. First, at an academic level the use of a novel approach (IPM) to ask a number of questions, as outlined here provides new insight into ungulate demography and evolution. The papers published through this Fellowship will be well cited by the Fellow’s peers.

At an applied level, the methods outlined in the generalised ungulate IPM can be replicated for other taxa, such as birds, or even across vertebrates. While the model remains to be validated, it does seem that a generalised model is possible to build, and while we don’t recommend that such a general model be used as a basis for management, it does allow for sensitivity analysis, that in turn guides field data collection, thereby saving managers substantial funds.

Our work on simulating hunting in bighorn sheep has substantial applied ramifications. The results suggest that sport hunting only drives a shift in body size, or possibly horn size, in hunted ungulates when the trait is heritable. If this is not the case, then hunting may drive a change in the targeted trait, but most likely through disruption to age and sex structure. Thus, wildlife managers, as always need to monitor hunted populations and as best they can collate data on population structure.

The students supervised by the Fellow also produced research relevant to broader society, in particular the finding that across sub-Saharan Africa, elephants have been subjected to such substantial hunting and poaching pressure that a marked decline in mean male and female tusk size has occurred.

Of interest, the Fellow has presented these findings at a number of conferences, including the Southern African Wildlife Management annual meeting and the Savanna Science Network Meeting. Both of these conferences bring together both scientists and wildlife managers, and the Fellows work was well-received at both venues.

References cited

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